

The stable isotope archive of Lake Pannon as a mirror of Late Miocene climate change

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Abstract

Lake Pannon was a long-lived Miocene and Pliocene lake system in Central Europe with a famous endemic mollusc fauna. The radiation of melanopsid gastropods and dreissenid bivalves has been explained simply by the opportunity to settle empty ecological niches after the extinction of marine life at the end of the Middle Miocene. This model, however, fails to explain the offset in the timings of evolutionary pulses in different mollusc families. Stable isotope data (oxygen, carbon) indicate a strong climatic forcing on these radiations. Moreover, the investigated time span covers the well-known Vallesian optimum and subsequent crises in European terrestrial ecosystems during the Late Miocene. The new palaeoclimatic data on the strongly changing isotope patterns of mollusc aragonite of Lake Pannon might shed light on the mechanisms acting during this crucial period.

According to the new interpretation, the early lake (~11.6 Ma) was still influenced by the latest Middle Miocene dry spell. This phase coincided with a pronounced radiation of melanopsid gastropods. During the warm early Late Miocene (~10 Ma) humidity increased and culminated in a phase with high summer precipitation. This caused a reorganisation of the coastal–deltaic faunas, suppressing the radiation of melanopsids. On the other hand, high nutrient loads favoured the dispersion of filter-feeding dreissenids.

Despite steadily declining salinity, Lake Pannon remained an alkaline lake with pronounced stratification that was apparently periodically disrupted only during the humid early Late Miocene. A separation of the isotope data into genera and ecological guilds is the prerequisite for discussing overall trends of long-lived lake systems.

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1. Introduction

At the boundary between the Middle Miocene and the Late Miocene, central and south-eastern Europe experienced a geographic reorganisation. The Para-

tethys Sea – an epicontinental sea that formed since Oligocene times in the north of the ascending Alpidic mountain chains – became disintegrated and fell apart into a lake system in the west and a strongly cut-off sea in the east (Fig. 1A; Rögl, 1998; Popov et al., 2004). The western lake system covered the Pannonian back-arc basins complex and is therefore called Lake Pannon (Fig. 1B; Magyar et al., 1999). In its initial phase, roughly at 11.6 Ma, the lake was encircled by the Alps,

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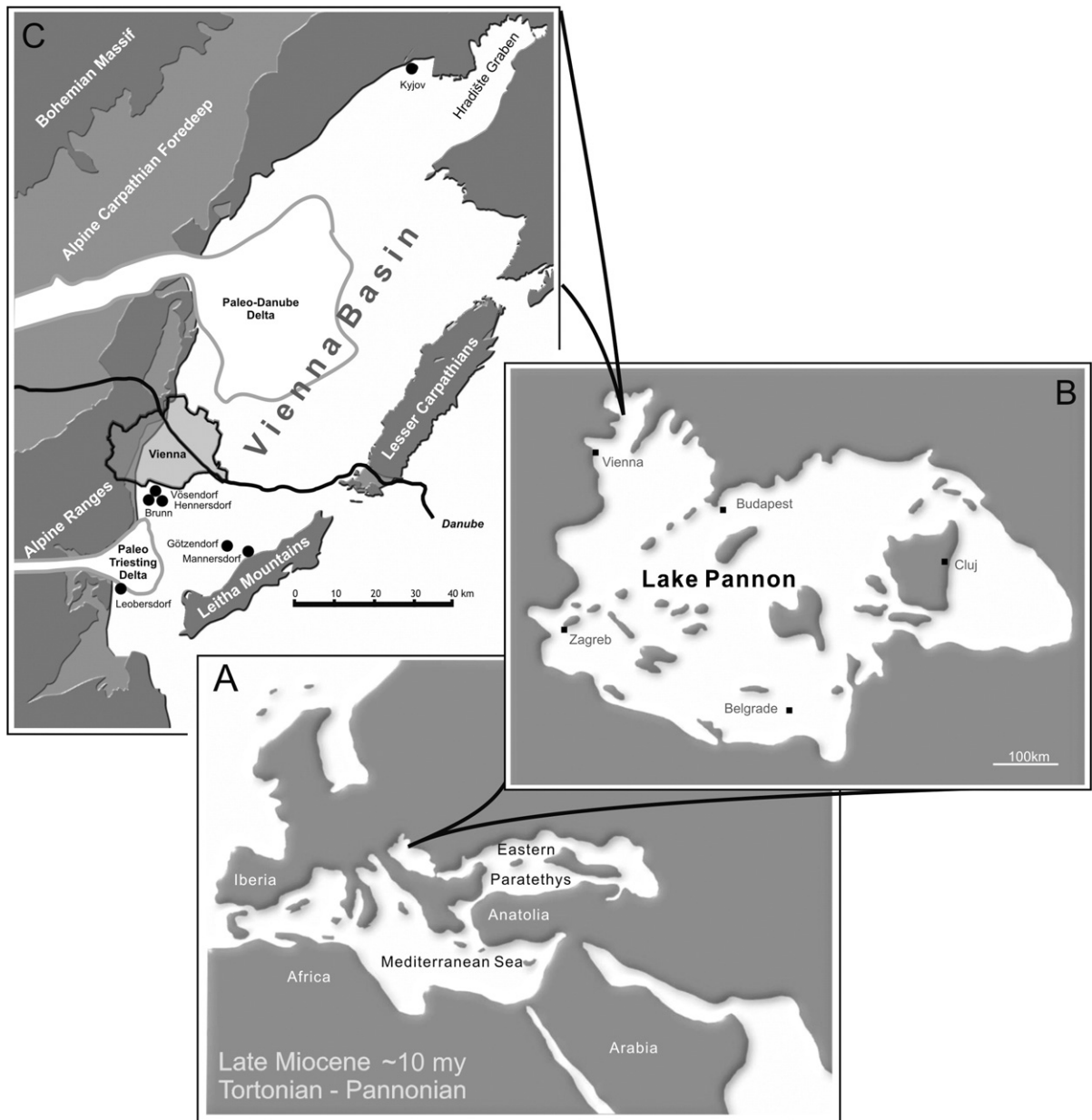


Fig. 1. Palaeogeographic and geographic situation of the investigation area. Insert A shows the position of Lake Pannon in the Late Miocene world (modified after Rögl, 1998 and Popov et al., 2004), B shows the outline of the lake during the middle Pannonian when it reached its maximum extent (after Magyar et al., 1999). Insert C illustrates the Vienna Basin, the position of palaeo-deltas and the position of sampling localities (after Harzhauser et al., 2004).

the Carpathians and the Dinarids. It reached its maximum extent during the Pannonian (\approx Tortonian) at about 10 Ma. Soon after, it started to shrink in several phases and the coastline retreated from its northwestern part (Magyar et al., 1999). The central and southern part remained as a several-hundred-meters deep subbasin complex filled by prodelta turbidities and prograding deltaic deposits (Popov et al., 2004).

Little is known about the palaeolimnology of Lake Pannon. A manifold succession of mollusc associations was defined by Korpás-Hódi (1983) inhabiting the shores of the lake and the sublittoral zone down to about 80 m water depth. At least seasonally, a stratified water body with an oxygen-deficient hypolimnion developed (Harzhauser and Mandić, 2004; Magyar et al., 2006). The wave-base was established at about 10–15 m depth

(Korpás-Hódi, 1983). Many authors have discussed the water chemistry and especially the salinity of Lake Pannon. The assumptions were mainly based on the mollusc and ostracod fauna. Hence, Papp (1953) calculated an initial salinity of 15 psu for Lake Pannon. During the maximum extant of the lake salinities between 10 and 12 psu were inferred by Korpás-Hódi (1983) based on the mollusc associations. In its latest stage all authors suggest salinities of about 0.5 psu for Lake Pannon due to the increasing freshwater discharge. Fossil-water analyses of well-logs support this interpretation (Mátyás et al., 1996).

The problem, however, is that the highly endemic fauna with extinct taxa such as *Congerina* and *Sinucongeria* complicates a straightforward actualistic approach. This situation is perhaps most obvious for offshore environments because only very few mollusc species were adapted to the often dysoxic conditions in the deeper lake (see also Harzhauser and Mandic, 2004). Gastropods in particular are poorly suited for reconstructions of deeper lake environments because only few of them inhabited the muddy bottom. Stable isotope studies to analyze Lake Pannon environments are one approach to overcoming this problem. The two outstanding basic papers by Geary et al. (1989) and Mátyás et al. (1996) provide 87 measurements derived from mollusc shells from the Late Miocene of that lake. Whilst Geary et al. (1989) focused their study on melanopsid gastropods, Mátyás et al. (1996) presented a wide range of bivalve taxa with the emphasis on lymnardiids and dreissenids. These studies shed light on the general isotope composition in Lake Pannon in respect to its isotope-heritage from its ancestor, the marine Paratethys Sea. Secondly, they deciphered salinity drops during the Late Miocene at the Pannonian/Pontian transition. Isochronous, habitat-related differences in the isotope patterns between the species and ecological guilds, however, were beyond the scope of these studies. The present investigation elucidates this aspect of Lake Pannon's faunal history.

The excellent preservation of metastable aragonite in the studied shells has been used to argue that the isotopic composition is also primary. Additionally, molluscs are considered to precipitate their shells in isotopic equilibrium (Grossman and Ku, 1986). So it may be reasonably assumed that the isotopic composition of the analyzed aragonitic shells reflects the temperature and the isotopic composition of the ambient water. The main controlling factors of $\delta^{18}\text{O}$ values in mollusc shells are temperature and the $\delta^{18}\text{O}$ of the ambient water. $\delta^{18}\text{O}$ values of the freshwater are controlled by the isotopic composition of the rainwater and by the precipitation/

evaporation ratio. In contrast, $\delta^{13}\text{C}$ values of marine and freshwater molluscs are influenced by a multitude of factors, e.g., upwelling, seasonal productivity, diet, living mode, growth rate, reproductive status (Geary et al., 1989 cum lit., Bonadonna et al., 1999). The observed isotope composition is therefore a result of a very complex interaction of vital effects and environmental parameters. Nevertheless, several studies have documented the value of mapping the isotope signatures of palaeoenvironments on a broad scale by measuring a multitude of coeval species with different ecological requirements (e.g., Purton and Brasier, 1997; Latal et al., 2004, 2005).

2. Material and palaeogeographic setting of the sections

A total of 36 bivalve specimens were analyzed for oxygen and carbon isotopes, yielding 117 data-pairs (Table 1). Only pristine aragonite shells were sampled. For stable isotope analyses, the shells were sampled with a 0.3-mm drill. Sample density depended on shell size. Oxygen and carbon isotopes were determined by the reaction of the samples with 100% phosphoric acid at 70 °C in a Finnigan Kiel II automated reaction system, and measured with a Finnigan Delta Plus isotope-ratio mass spectrometer at the Institute of Earth Sciences, University of Graz. Measurements of NBS-19 and an internal laboratory standard yielded a standard deviation of 0.1‰ for both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$. Isotope data are given in ‰ relative to VPDB.

To cover a maximum spectrum of ecological requirements, presumably freshwater-dwelling unionids such as *Margaritifera flabellatiformis* and *Unio atavus* were incorporated along with typical Lake Pannon inhabitants of the genera *Mytilopsis* (6 species) and *Congerina* (3 species). In addition, 87 data-pairs from melanopsid gastropods, lymnardiid bivalves and some dreissenids were incorporated from Geary et al. (1989) and Mátyás et al. (1996).

Most shells were collected in lower to upper Pannonian fluvial to lacustrine deposits of the Vienna Basin. The biostratigraphic position of the samples is deduced from the well-log supported concepts of Papp (1953) and integrated into the age-model of Harzhauser et al. (2004). Consequently, the samples fall into three groups representing parts of the early Pannonian (~11.4–11.0 Ma), the middle Pannonian (~10.5–10.3 Ma) and the late Pannonian (~9.8 Ma and younger). Taxa and localities are summarized below; the first number in parenthesis represents the number of specimens per species used for the isotope analysis; the

Table 1

Data sheet of all measured specimens (isotope data are given in ‰ relative to VPDB); the stratigraphic correlation follows Harzhauser et al. (2004)

Sample #	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	Species	Locality	Stage
Cong 15-1	-10.5	-7.1	<i>Margaritifera flabellatiformis</i>	Götzendorf, A	Pannonian F
Cong 15-2	-11.2	-6.9	<i>Margaritifera flabellatiformis</i>	Götzendorf, A	Pannonian F
Cong 15-3	-10.8	-7.2	<i>Margaritifera flabellatiformis</i>	Götzendorf, A	Pannonian F
Cong 19-1	-2.6	-5.2	<i>Unio atavus</i>	Vösendorf, A	Pannonian E
Cong 19-2	-2.1	-4.5	<i>Unio atavus</i>	Vösendorf, A	Pannonian E
Cong 19-3	-2.1	-5.4	<i>Unio atavus</i>	Vösendorf, A	Pannonian E
Cong 28-1	-1.9	1.1	<i>Unio atavus</i>	Kyjov, Cs	Pannonian BC
Cong 28-2	-2.3	1.3	<i>Unio atavus</i>	Kyjov, Cs	Pannonian BC
Cong 28-3	-2.4	-0.4	<i>Unio atavus</i>	Kyjov, Cs	Pannonian BC
Cong 31-1	-0.7	-0.4	<i>Unio atavus</i>	Brunn, A	Pannonian E
Cong 31-2	-1.9	1.2	<i>Unio atavus</i>	Brunn, A	Pannonian E
Cong 31-3	-2.5	-8.4	<i>Unio atavus</i>	Brunn, A	Pannonian E
Cong 32-1	-1.9	-3.9	<i>Unio atavus</i>	Brunn, A	Pannonian E
Cong 32-2	-1.6	-2.7	<i>Unio atavus</i>	Brunn, A	Pannonian E
Cong 32-3	-1.6	-1.9	<i>Unio atavus</i>	Brunn, A	Pannonian E
Cong 12-1	-0.8	1.5	<i>Mytilopsis ornithopsis</i>	Leobersdorf, A	Pannonian B
Cong 12-2	-0.9	1.9	<i>Mytilopsis ornithopsis</i>	Leobersdorf, A	Pannonian B
Cong 12-3	-0.8	2.4	<i>Mytilopsis ornithopsis</i>	Leobersdorf, A	Pannonian B
Cong 13-1	-0.4	2.2	<i>Mytilopsis ornithopsis</i>	Leobersdorf, A	Pannonian B
Cong 13-2	-0.2	2.8	<i>Mytilopsis ornithopsis</i>	Leobersdorf, A	Pannonian B
Cong 13-3	-1.3	2.3	<i>Mytilopsis ornithopsis</i>	Leobersdorf, A	Pannonian B
Cong 14-1	-1.1	0.2	<i>Mytilopsis ornithopsis</i>	Leobersdorf, A	Pannonian B
Cong 14-2	-0.4	1.1	<i>Mytilopsis ornithopsis</i>	Leobersdorf, A	Pannonian B
Cong 14-3	-0.9	1.4	<i>Mytilopsis ornithopsis</i>	Leobersdorf, A	Pannonian B
Cong 14-4	-1.2	2.3	<i>Mytilopsis ornithopsis</i>	Leobersdorf, A	Pannonian B
Cong 25-27	-1.4	1.9	<i>Mytilopsis scrobiculata</i>	Kyjov, Cs	Pannonian BC
Cong 1-1	-0.6	0.6	<i>Mytilopsis hoernesii</i>	Kyjov, Cs	Pannonian C
Cong 1-2	-0.9	0.6	<i>Mytilopsis hoernesii</i>	Kyjov, Cs	Pannonian C
Cong 1-3	-0.3	0.8	<i>Mytilopsis hoernesii</i>	Kyjov, Cs	Pannonian C
Cong 2-1	-0.7	1.4	<i>Mytilopsis hoernesii</i>	Kyjov, Cs	Pannonian C
Cong 2-2	-0.7	0.5	<i>Mytilopsis hoernesii</i>	Kyjov, Cs	Pannonian C
Cong 2-3	-0.7	0.0	<i>Mytilopsis hoernesii</i>	Kyjov, Cs	Pannonian C
Cong 2-4	-0.4	0.5	<i>Mytilopsis hoernesii</i>	Kyjov, Cs	Pannonian C
Cong 3-1	-0.1	0.4	<i>Mytilopsis hoernesii</i>	Kyjov, Cs	Pannonian C
Cong 3-2	-0.3	0.4	<i>Mytilopsis hoernesii</i>	Kyjov, Cs	Pannonian C
Cong 3-3	-1.3	1.3	<i>Mytilopsis hoernesii</i>	Kyjov, Cs	Pannonian C
Cong 6-1	-1.2	1.6	<i>Mytilopsis spathulata</i>	Leobersdorf, A	Pannonian E
Cong 6-2	-1.8	0.5	<i>Mytilopsis spathulata</i>	Leobersdorf, A	Pannonian E
Cong 6-3	-1.9	0.7	<i>Mytilopsis spathulata</i>	Leobersdorf, A	Pannonian E
Cong 6-4	-1.2	1.3	<i>Mytilopsis spathulata</i>	Hennersdorf, A	Pannonian E
Cong 7-1	-1.9	1.0	<i>Mytilopsis spathulata</i>	Hennersdorf, A	Pannonian E
Cong 7-2	-2.6	0.4	<i>Mytilopsis spathulata</i>	Hennersdorf, A	Pannonian E
Cong 7-3	-3.4	-0.9	<i>Mytilopsis spathulata</i>	Hennersdorf, A	Pannonian E
Cong 20-1	-1.2	0.4	<i>Mytilopsis spathulata</i>	Vösendorf, A	Pannonian E
Cong 20-2	-1.7	-0.2	<i>Mytilopsis spathulata</i>	Vösendorf, A	Pannonian E
Cong 20-3	-1.4	0.0	<i>Mytilopsis spathulata</i>	Vösendorf, A	Pannonian E
Cong 20-4	-2.0	0.3	<i>Mytilopsis spathulata</i>	Vösendorf, A	Pannonian E
Cong 21-1	-0.4	-0.2	<i>Mytilopsis spathulata</i>	Vösendorf, A	Pannonian E
Cong 21-2	-0.7	0.6	<i>Mytilopsis spathulata</i>	Vösendorf, A	Pannonian E
Cong 21-3	-1.3	-0.9	<i>Mytilopsis spathulata</i>	Vösendorf, A	Pannonian E
Cong 36-1	-1.2	0.2	<i>Mytilopsis spathulata</i>	Brunn, A	Pannonian E
Cong 36-2	-2.6	-0.4	<i>Mytilopsis spathulata</i>	Brunn, A	Pannonian E
Cong 36-3	-1.5	0.2	<i>Mytilopsis spathulata</i>	Brunn, A	Pannonian E
Cong 36-4	-0.6	-0.1	<i>Mytilopsis spathulata</i>	Brunn, A	Pannonian E
Cong 37-1	-1.1	0.2	<i>Mytilopsis spathulata</i>	Brunn, A	Pannonian E
Cong 37-2	-0.8	-0.4	<i>Mytilopsis spathulata</i>	Brunn, A	Pannonian E

Table 1 (continued)

Sample #	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	Species	Locality	Stage
Cong 37-3	-1.2	-0.1	<i>Mytilopsis spathulata</i>	Brunn, A	Pannonian E
Cong 37-4	0.9	0.8	<i>Mytilopsis spathulata</i>	Brunn, A	Pannonian E
Cong 38-1	-3.1	-0.1	<i>Mytilopsis spathulata</i>	Brunn, A	Pannonian E
Cong 38-2	-2.9	0.3	<i>Mytilopsis spathulata</i>	Brunn, A	Pannonian E
Cong 38-3	-2.6	0.6	<i>Mytilopsis spathulata</i>	Brunn, A	Pannonian E
Cong 39-1	-3.4	-0.1	<i>Mytilopsis spathulata</i>	Brunn, A	Pannonian E
Cong 39-2	-2.5	0.3	<i>Mytilopsis spathulata</i>	Brunn, A	Pannonian E
Cong 39-3	-1.7	-0.4	<i>Mytilopsis spathulata</i>	Brunn, A	Pannonian E
Cong 16-1	-8.7	-7.2	<i>Mytilopsis neumayri</i>	Götzendorf, A	Pannonian F
Cong 16-2	-10.2	-7.6	<i>Mytilopsis neumayri</i>	Götzendorf, A	Pannonian F
Cong 16-3	-10.3	-8.3	<i>Mytilopsis neumayri</i>	Götzendorf, A	Pannonian F
Cong 17-1	-10.5	-6.5	<i>Mytilopsis neumayri</i>	Götzendorf, A	Pannonian F
Cong 17-2	-8.6	-6.0	<i>Mytilopsis neumayri</i>	Götzendorf, A	Pannonian F
Cong 17-3	-10.9	-8.1	<i>Mytilopsis neumayri</i>	Götzendorf, A	Pannonian F
Cong 18-1	-9.1	-6.9	<i>Mytilopsis neumayri</i>	Götzendorf, A	Pannonian F
Cong 18-2	-8.7	-5.8	<i>Mytilopsis neumayri</i>	Götzendorf, A	Pannonian F
Cong 29-1	-2.8	-0.4	<i>Mytilopsis croatica</i>	Zagreb, Cr	"Pontian"
Cong 29-2	-2.8	0.2	<i>Mytilopsis croatica</i>	Zagreb, Cr	"Pontian"
Cong 29-3	-3.0	0.6	<i>Mytilopsis croatica</i>	Zagreb, Cr	"Pontian"
Cong 30-1	-2.9	-0.2	<i>Mytilopsis croatica</i>	Zagreb, Cr	"Pontian"
Cong 30-2	-2.7	0.0	<i>Mytilopsis croatica</i>	Zagreb, Cr	"Pontian"
Cong 30-3	-2.7	0.1	<i>Mytilopsis croatica</i>	Zagreb, Cr	"Pontian"
Cong 4-1	0.2	2.7	<i>Congeria partschi</i>	Leobersdorf, A	Pannonian C
Cong 4-2	0.2	0.7	<i>Congeria partschi</i>	Leobersdorf, A	Pannonian C
Cong 4-3	0.8	1.3	<i>Congeria partschi</i>	Leobersdorf, A	Pannonian C
Cong 4-4	0.3	1.5	<i>Congeria partschi</i>	Leobersdorf, A	Pannonian C
Cong 5-1	0.8	2.2	<i>Congeria partschi</i>	Leobersdorf, A	Pannonian C
Cong 5-2	1.0	1.5	<i>Congeria partschi</i>	Leobersdorf, A	Pannonian C
Cong 5-3	0.6	1.9	<i>Congeria partschi</i>	Leobersdorf, A	Pannonian C
Cong 5-4	0.6	2.0	<i>Congeria partschi</i>	Leobersdorf, A	Pannonian C
Cong 10-1	0.7	1.4	<i>Congeria zsigmondyi</i>	Mannersdorf, A	Pannonian E
Cong 10-2	0.7	1.9	<i>Congeria zsigmondyi</i>	Mannersdorf, A	Pannonian E
Cong 10-3	0.8	1.8	<i>Congeria zsigmondyi</i>	Mannersdorf, A	Pannonian E
Cong 11-1	-1.4	0.3	<i>Congeria zsigmondyi</i>	Mannersdorf, A	Pannonian E
Cong 11-2	0.9	0.8	<i>Congeria zsigmondyi</i>	Mannersdorf, A	Pannonian E
Cong 11-3	1.0	1.2	<i>Congeria zsigmondyi</i>	Mannersdorf, A	Pannonian E
Cong 8-1	0.4	0.5	<i>Congeria subglobosa</i>	Hennersdorf, A	Pannonian E
Cong 8-2	0.4	0.7	<i>Congeria subglobosa</i>	Hennersdorf, A	Pannonian E
Cong 8-3	0.3	0.8	<i>Congeria subglobosa</i>	Hennersdorf, A	Pannonian E
Cong 9-1	-0.6	0.0	<i>Congeria subglobosa</i>	Hennersdorf, A	Pannonian E
Cong 9-2	-0.4	-0.3	<i>Congeria subglobosa</i>	Hennersdorf, A	Pannonian E
Cong 9-3	-0.5	-1.2	<i>Congeria subglobosa</i>	Hennersdorf, A	Pannonian E
Cong 9-4	0.0	-0.2	<i>Congeria subglobosa</i>	Hennersdorf, A	Pannonian E
Cong 23-1	-0.6	0.2	<i>Congeria subglobosa</i>	Vösendorf, A	Pannonian E
Cong 23-2	-0.1	0.7	<i>Congeria subglobosa</i>	Vösendorf, A	Pannonian E
Cong 23-3	-0.2	0.5	<i>Congeria subglobosa</i>	Vösendorf, A	Pannonian E
Cong 23-4	-1.3	-0.2	<i>Congeria subglobosa</i>	Vösendorf, A	Pannonian E
Cong 24-1	-0.8	-0.2	<i>Congeria subglobosa</i>	Vösendorf, A	Pannonian E
Cong 24-2	-0.4	-0.7	<i>Congeria subglobosa</i>	Vösendorf, A	Pannonian E
Cong 24-3	-0.4	0.0	<i>Congeria subglobosa</i>	Vösendorf, A	Pannonian E
Cong 24-4	-0.7	0.1	<i>Congeria subglobosa</i>	Vösendorf, A	Pannonian E
Cong 33-1	-2.4	1.4	<i>Congeria subglobosa</i>	Brunn, A	Pannonian E
Cong 33-2	-2.4	1.5	<i>Congeria subglobosa</i>	Brunn, A	Pannonian E
Cong 33-3	-2.5	1.1	<i>Congeria subglobosa</i>	Brunn, A	Pannonian E
Cong 33-4	-3.0	0.9	<i>Congeria subglobosa</i>	Brunn, A	Pannonian E
Cong 34-1	-1.3	-3.8	<i>Congeria subglobosa</i>	Brunn, A	Pannonian E
Cong 34-2	-0.7	-1.9	<i>Congeria subglobosa</i>	Brunn, A	Pannonian E
Cong 34-3	-0.6	-1.2	<i>Congeria subglobosa</i>	Brunn, A	Pannonian E

(continued on next page)

Table 1 (continued)

Sample #	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	Species	Locality	Stage
Cong 35-1	-1.3	-0.3	<i>Congeria subglobosa</i>	Brunn, A	Pannonian E
Cong 35-2	-0.8	0.4	<i>Congeria subglobosa</i>	Brunn, A	Pannonian E
Cong 35-3	-0.5	0.7	<i>Congeria subglobosa</i>	Brunn, A	Pannonian E

Additional data used in this study have been published in Geary et al. (1989) and Mátyás et al. (1996).

second number indicates the number of samples obtained from the specimens.

1. The early Pannonian is represented by *U. atavus* (1/3), *Mytilopsis hoernesii* (3/10) and *Mytilopsis scrobiculata* (1/3) from Kyjov (Czech Republic) in the northern Vienna Basin (Fig. 1C). There, in the Hradište Graben, a small lagoon or embayment of Lake Pannon formed. A small river that entered the lagoon at its northern tip provided fluvial influx. Coeval samples of *Mytilopsis ornithopsis* (3/10) and *Congeria partschi* (2/8) from Leobersdorf (Austria) in the southern basin part derive from coarse clastic marginal deposits. Freshwater discharge is also documented for that section, which was in the sphere of influence of the delta of the Palaeo-Triesting River (Fig. 1C; Harzhauser et al., 2004).

This data set was enlarged by the published isotope records for *Melanopsis fossilis* from Föllik (Austria) (Geary et al., 1989).

2. The mid-Pannonian interval (Pannonian zone E sensu Papp, 1953) is best documented. From the Austrian localities Vösendorf, Hennersdorf, Brunn, and Leobersdorf (Fig. 1C) to the south of Vienna, shells of *U. atavus* (3/9), *Mytilopsis spathulata* (8/28) and *Congeria subglobosa* (7/25) were analyzed. Published values for several *Melanopsis vindobonensis* from Hennersdorf were taken from Geary et al. (1989; these shells erroneously dated as early Pannonian in that study). The palaeogeographic position was about 3–4 km off the western shores of Lake Pannon. All species of *Congeria* and *M. spathulata* are frequently found in situ or display only minor within-habitat transport (Harzhauser and Mandic, 2004). In contrast, *M. vindobonensis* and *U. atavus* are restricted to silty–sandy lenses reflecting out-of-habitat occurrences, probably by storm-induced transport from the coastal areas. Coeval shells of *Congeria zsigmondyi* (2/6) were collected at Mannersdorf (Austria) in the southern Vienna Basin. The section represents a basinal facies from the eastern part of the southern Vienna Basin (Fig. 1C). The dark-grey pelites yielding the dreissenid shells were deposited about 1 km northwest off the coast. Additional data for various lymnocyprids from Hungarian well-cores were utilized from Mátyás et al. (1996).

3. Late Pannonian data are based on the shells of the unionid *M. flabellatiformis* (1/3) and of the dreissenid

Mytilopsis neumayri (3/8) from the Götzendorf section in Austria (Fig. 1C). These fluvial and lacustrine deposits of the Éáry Formation formed on a floodplain of the Palaeo-Danube during the late Pannonian (Harzhauser and Tempfer, 2004). All shells derive from a crevasse splay coquina. Based on the mollusc and amphibian assemblages, Harzhauser and Tempfer (2004) interpreted a fast-flowing, cool, oligotrophic, calcium-deficient tributary of the Palaeo-Danube as the habitat of the studied bivalves.

Additional late Pannonian data were obtained from *Mytilopsis croatica* (2/6) from Zagreb (Cr). Other data for *Congeria praerhomboides*, *Mytilopsis zagrabensis*, *M. balatonica*, *Melanopsis pygmaea* and *Melanopsis bouei* have been incorporated from Mátyás et al. (1996) and Geary et al. (1989). These deposits are partly considered as Pontian in the literature, but the use of the term Pontian within Lake Pannon deposits is problematic (Magyar et al., 1999). Consequently, the late Pannonian spans a rather broad but poorly defined time interval.

These literature-based late Pannonian taxa are usually littoral to sublittoral elements of Lake Pannon. The positions of the sections taken from the literature are indicated in Geary et al. (1989) and Mátyás et al. (1996); they are mainly located within the Vienna/Budapest/Zagreb triangle in Fig. 1B.

3. Results

All isotope data are plotted within the stratigraphic framework for the Pannonian of the Vienna Basin (Fig. 2). The stratigraphic position of the sections follows Harzhauser et al. (2004), spanning an interval of about 2 Ma. The partly problematic Pontian and late Pannonian literature-based data are plotted within a single time interval. This enables a visualization of total ranges and trends for both stable isotopes. Early Pannonian $\delta^{18}\text{O}$ values ranged from -3 to +1‰. Within that spectrum, the lower values are contributed by unionids and melanopsids, whereas the dreissenids yield the higher values. This structure continues into the middle Pannonian, which displays a wider range of $\delta^{18}\text{O}$ from -3.9 to +0.9‰, with a single outlier of -5.6‰. The late Pannonian samples document a shift

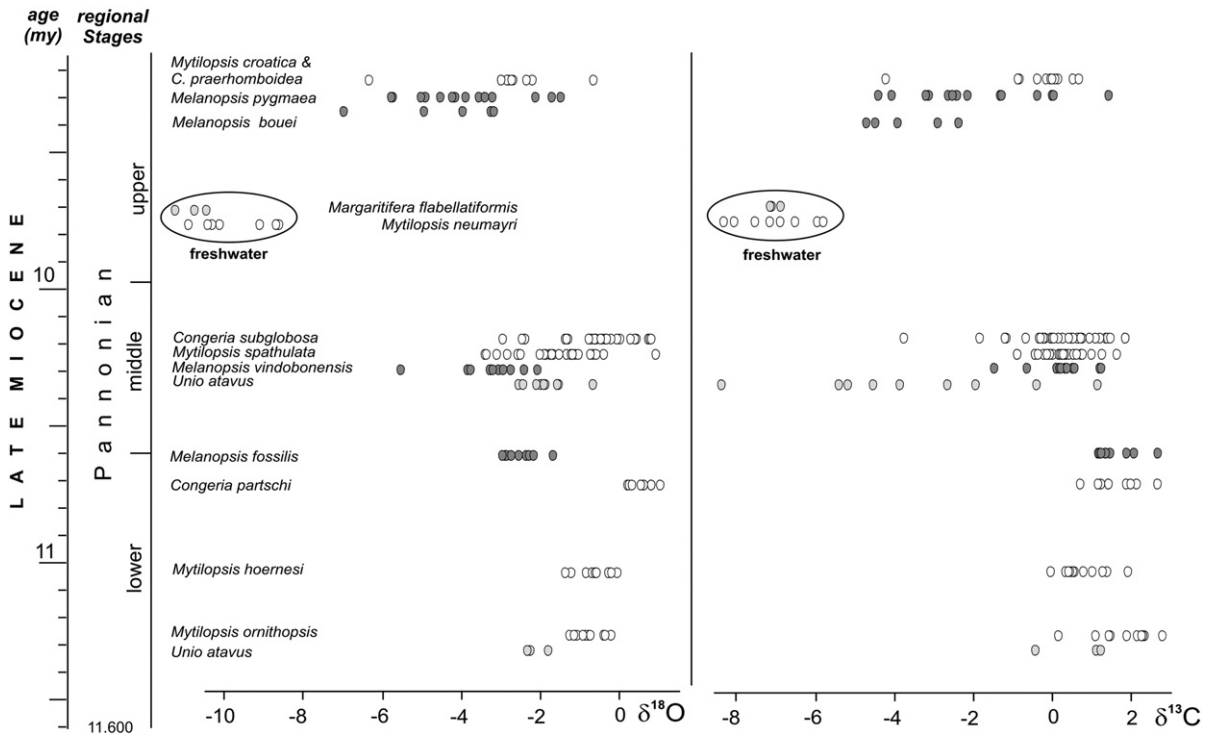


Fig. 2. Stratigraphic correlation of the isotope data (tentative for the upper Pannonian); white circles=dreissenids, dark grey=*Melanopsis*, light grey=unionids. Pure freshwater values are represented by *Mytilopsis neumayri* and *Margaritifera flabellatiformis*, which were collected from riverine deposits about 100 km in the hinterland of Lake Pannon, excluding any influence of Lake Pannon waters.

towards lighter values in the range from -7 to -0.7 ‰. Nonetheless, these values are heavier than the ranges of the late Pannonian freshwater end-member with pure freshwater signatures (-11.2 to -8.6 ‰).

The carbon record is fairly similar. The heavy early Pannonian values for $\delta^{13}\text{C}$ (-0.4 to $+2.8$ ‰) are followed by a much wider range of middle Pannonian values (-5.4 to $+1.5$ ‰; except for an outlier of -8.4 ‰) and late Pannonian ones (-4.7 to $+1.5$ ‰). Again, these data differ considerably from the light values of the freshwater group (-8.3 to -4.2 ‰).

The weighting of the data within those ranges, which are controlled by extreme values, is more evident in the value–frequency diagram (Fig. 3). For both isotopes the scatter of values increases with time in the Pannonian. This trend is not solely a taxonomic effect because the same genera are incorporated in each interval, although in varying proportions. For the pooled data the oxygen curves of the early and middle Pannonian are quite similar, with pronounced value–frequency maxima between -2.0 and 1.0 ‰ (Fig. 3). A considerable shift of value–frequencies towards lighter values occurs in the late Pannonian data set, when these maxima of the value–frequency curve range between -5.0 and -2.0 ‰. The carbon signatures of the value–frequency

diagram display even more pronounced maxima. Earlier than the oxygen signals, the carbon curve already shows a slight shift towards lighter values in the middle Pannonian. The maximum moves from roughly $+1.0$ to $+3.0$ ‰ in the early Pannonian to around 0 ‰ in the middle Pannonian. In the late Pannonian the maximum lies between 0.0 and -1.0 ‰, with several smaller peaks between -2.0 and -8.0 ‰.

4. Discussion

4.1. The impact of mollusc life-strategies and habitat preferences on expected isotope signatures

4.1.1. The Pannonian freshwater end-member

The Late Miocene freshwater end-member is represented by *M. flabellatiformis* and *M. neumayri* found in 9.8-Ma-old fluvial crevasse splay deposits (Harzhauser and Tempfer, 2004). The setting was part of the wetland system surrounding the Palaeo-Danube. At that time the shores of Lake Pannon had already shifted more than 100 km towards the south-east into today's Hungarian territory (Harzhauser et al., 2004).

The frequent *M. flabellatiformis* is highly significant for riverine freshwater. Its modern congener is the

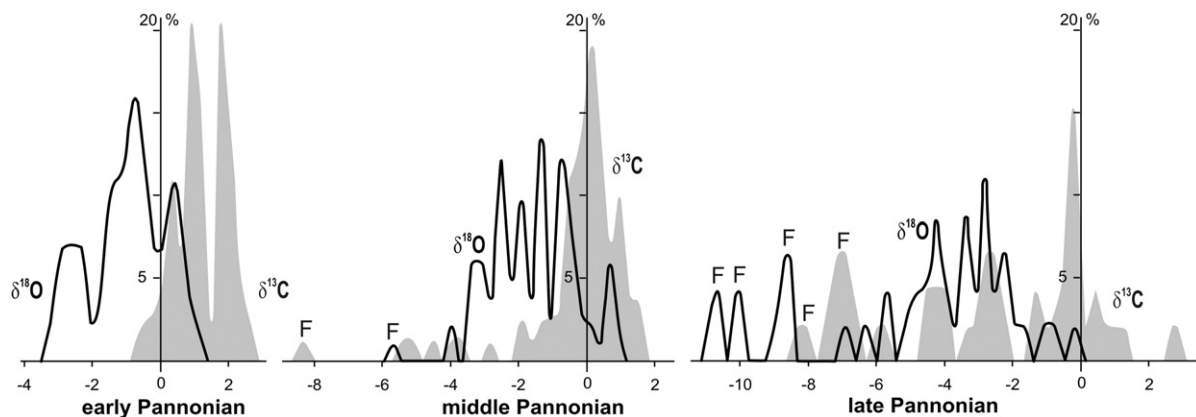


Fig. 3. Value–frequency diagrams for three time intervals in percentage based on the data in Table 1. Black lines are $\delta^{18}\text{O}$ values, grey area represents carbon isotopes; F indicates pure freshwater taxa. Note the clear shift towards depleted values for the maxima in both stable isotopes. Whilst the oxygen isotope signal shifted considerably in the late Pannonian, suggesting a further drop in salinity, the carbon isotope maxima remained quite high, as expected in alkaline lakes.

freshwater pearl mussel *Margaritifera margaritifera*, attaining individual ages of more than 100 years. This species burrows into sandy substrates, often between boulders and pebbles. It is indicative for fast-flowing, oligotrophic, calcium-deficient rivers and streams. *M. margaritifera* requires cool, well-oxygenated water and shuns turbidity and hard water. Highest mussel densities are associated with shaded channels and shallow channel depths from 1 to 3 m (all data from Bauer, 1988; Valovirta, 1995; Gittings et al., 1998; Geist et al., 2005). Based on these requirements and on the co-occurrence of the fossil species, including the sensitive amphibian *Andrias scheuchzeri*, Harzhauser and Tempfer (2004) reconstructed a well-flowing, oxygenated river with swift currents, clear water and bottoms with rocky crevices for the Götzendorf section. The same palaeoenvironmental conditions are assumed for the syntopic *M. neumayri*.

Hence, based on the synecological and sedimentological data, the dreissenid *M. neumayri* and the unionid *M. flabellatiformis* are good candidates to reveal the isotope composition of a riverine Pannonian freshwater end-member. Both do in fact show a good overlap in data: $\delta^{13}\text{C}$ of *M. neumayri* ranges between -8.3 and -5.8‰ ; its $\delta^{18}\text{O}$ is between -10.9 and -8.6‰ . *M. flabellatiformis* displays $\delta^{13}\text{C}$ records between -7.2‰ and -6.9‰ and $\delta^{18}\text{O}$ of -11.2 to -10.4‰ .

These Pannonian riverine $\delta^{13}\text{C}$ values are generally slightly heavier than those of modern unionids from temperate regions. Extant *M. margaritifera* have been documented by Geist et al. (2005) to have $\delta^{13}\text{C}$ ranges of up to 5‰ between -10 and -15‰ due to strong metabolic influences. A comparable variation from -9

to -14.5‰ (Veinott and Cornett, 1998) and -11 to -14‰ (Fastovsky et al., 1993) was shown for *Elliptio complanata*. Shells of recent *Anodonta cygnea* from the Rhine display $\delta^{13}\text{C}$ values ranging from -15.5 to -8.3‰ (Ricken et al., 2003). Extant dreissenids, however, display a much better overlap with *M. neumayri*. $\delta^{13}\text{C}$ values of *Dreissena polymorpha* are reported by Mitchell et al. (1995) to range from -8.1 to -6.4‰ in Oneida Lake (New York) and from -9.1 to -4.0‰ in the nearby Keuka Lake (Wurster and Patterson, 2001).

The oxygen values of the Pannonian freshwater end-member do not differ significantly from those reported for extant unionids of temperate lakes and rivers. The observed Pannonian range from -11.2 to -8.6‰ agrees well with data of *E. complanata* from Head Lake in Ontario (-10.2 to -6.2‰ ; Veinott and Cornett, 1996), *A. cygnea* from the Rhine ($\delta^{18}\text{O}$: -10.6 to -7.4‰), and *U. crassus nanus* from the Rhine ($\delta^{18}\text{O}$: -10.5 to -7.0‰ ; Ricken et al., 2003). The $\delta^{18}\text{O}$ range from -11.2 to -8.6‰ of the fingerclam *Sphaeridium simile* from Science Lake in New York also agrees with the above values, whilst *D. polymorpha* from Keuka Lake (New York) differs in having a heavier composition ($\delta^{18}\text{O}$: -8.6 to -4.1‰ ; Wurster and Patterson, 2001).

4.1.2. The transitional zone

Whereas the *Margaritifera* data are in good accordance with the expected freshwater signals, the data of the second unionid *U. atavus* are not. The $\delta^{18}\text{O}$ values (-2.6 to -0.7‰) are much heavier than those reported for the abovementioned extant unionids. Similarly, the observed $\delta^{13}\text{C}$ data (-8.4 to $+1.3\text{‰}$) tend to be heavier and display

a very large range ($>9\text{‰}$). These shells derive directly from Lake Pannon deposits in an assemblage with lymnocyprids and congerine bivalves. The frequent articulation of the valves of *U. atavus* contradicts stronger fluvial transport. Its late Pannonian descendant *Unio mihanovici* is interpreted by Korpás-Hódi (1983) and Müller and Szónoky (1990) to have settled shallow, aerated and agitated oligohaline waters in estuarine settings with salinities of up to 3‰. This would indicate a much better connection to Lake Pannon waters and should be reflected in an isotope signal closer to Lake Pannon shells than to the pure freshwater dwellers as represented by *M. flabellatiformis*.

Among extant unionids, comparable isotope patterns are mainly found in tropical and subtropical regions. Examples include the modern river-dwelling *Tripodion corrugatus* and the Miocene *Diplodon* aff. *longulus*. Both are from Amazonia and display wide ranges in $\delta^{18}\text{O}$ between -10.5 and -1.9‰ (Kaandorp et al., 2005). Equally, the modern Amazonian unionid *Anodontites trapesalis* has an extremely wide range in both isotopes; its $\delta^{18}\text{O}$ values vary between -9.9 and $+0.60\text{‰}$, the $\delta^{13}\text{C}$ data from -14.9 to -1.1‰ (Kaandorp et al., 2003). A corresponding scatter is also recorded by Dettman et al. (2001) for Miocene unionids from Nepal, with $\delta^{18}\text{O}$ between -10.8 and $+0.6\text{‰}$ and $\delta^{13}\text{C}$ between -11.8 and -2.3‰ .

Melanopsis is one of the mollusc genera exhibiting a tremendous endemic radiation in Lake Pannon (Papp, 1953). Geary et al. (1989) provided stable isotope data on *M. fossilis*, *M. vindobonensis*, *M. bouei*, and *M. pygmaea*. *M. bouei* is interpreted by Geary et al. (1989) as a freshwater dweller that might have also tolerated slightly higher salinities. *Melanopsis sturi*, as a direct descendant of *M. bouei*, is reported by Korpás-Hódi (1983) from lagoonal, partly swampy, quiet-water facies, indicating oligohaline to freshwater conditions. This interpretation fits to the requirements of extant representatives. The circum-Mediterranean *Melanopsis praemorsum* occupies a wide range of habitats, living in lakes, intertidal shores, estuaries, and marshes on mud, gravel and on subaquatic plants (Plaziat and Younis, 2005). In the estuary of the Crocodile River in Israel, *Melanopsis saulcyi* lives on organic matter, mud, and rocky substrate in up to 1 m water depth at salinities of up to 4‰ (Reinhardt et al., 2003). Two specimens collected by Reinhardt et al. (2003) at salinities of 2.6 and 3.2 psu displayed $\delta^{18}\text{O}$ values of -5.33 and -4.75‰ and $\delta^{13}\text{C}$ values of -8.99 and -8.79‰ . Fossil *Melanopsis impressa* from an early Miocene Paratethyan estuary show average $\delta^{18}\text{O}$ values of -8.7 and -5.3‰ for $\delta^{13}\text{C}$ (Latal et al., 2005; $n=15$). The

tendency of melanopsids to thrive in fluvial and estuarine environments suggests that their isotope signatures record the mixing line between freshwater and the coastal waters of Lake Pannon. Unsurprisingly, the entire *Melanopsis* data set therefore represents the largest ranges within the Pannonian samples, spanning $\delta^{18}\text{O}$ values from -7.0 to -1.4‰ and $\delta^{13}\text{C}$ values from -4.7 to $+2.7\text{‰}$.

4.1.3. Lake settings

Species of the dreissenid genera *Congeria* and *Mytilopsis* (according to the concept of Nuttall, 1990 and Harzhauser and Mandic, 2004) have been investigated. Based on actualistic approaches and various palaeoecological interpretations, the following autecological requirements of the involved taxa can be postulated.

Mytilopsis is a euryhaline genus comprising even mangrove swamp dwellers which may tolerate salinities of up to 25 psu (Ramachandra Raju et al., 1975; Archambault-Guezou, 1976; Laine et al., 2006). All species are filter-feeding, byssally attached epibionts living in the infralittoral or shallow sublittoral zone. Harzhauser and Mandic (2004) considered the Pannonian representatives as opportunistic *r*-strategists. $\delta^{18}\text{O}$ values of the measured *Mytilopsis* range from -3.0 to $+0.9\text{‰}$ and $\delta^{13}\text{C}$ values from -0.9 to $+2.8\text{‰}$.

Congeria species are semi-epifaunal, byssate sediment recliners which preferred aphytal habitats of the shallow to moderately deep sublittoral. They also occur in apparently oxygen- and nutrient-depleted environments of Lake Pannon and may be highly adapted *K*-strategists that even utilized chemosymbiosis (Harzhauser and Mandic, 2004). The large-sized, robust *Congeria* is frequently found in situ with valves articulated and the byssal/pedal gap pointing downward. *M. spathulata*, forming in situ colonies within empty *Congeria* shells, is also found within-habitat. Therefore, the stable isotope signatures of these taxa and related species will reflect the composition of the ambient sublittoral water of Lake Pannon. Consequently, *Congeria* species yield the heaviest isotope compositions in the entire data set ($\delta^{18}\text{O}$: -3.0 to $+1.0\text{‰}$; $\delta^{13}\text{C}$: -3.8 to $+2.7\text{‰}$).

4.2. Lake Pannon — a stratified alkaline lake

Lake Pannon is characterised by very high $\delta^{13}\text{C}$ values with pronounced maxima that shift only slightly throughout the Pannonian from $\sim+2$ to $\sim0\text{‰}$ (Fig. 3). These positive $\delta^{13}\text{C}$ maxima in the early and middle Pannonian exclude an acidic system. In modern lakes, such high $\delta^{13}\text{C}$ values strongly correlate with elevated

pH values (Bade et al., 2004). Within the empirical $\delta^{13}\text{C}/\text{pH}$ diagram of Bade et al. (2004) for extant lakes, the carbon signature of Lake Pannon would plot into the strongly alkaline field, suggesting an elevated pH value of 9–10. Comparable carbon regimes with $\delta^{13}\text{C}$ -peaks between +2 and -2‰ are frequently reported from the east African lakes; e.g., Lake Turkana (Kenia; pH ~10; Kallqvist et al., 1988), Lake Rukwa (Tanzania) in Talbot (1990) and Lake Tanganyika (Tanzania; pH ~9) in Dettman et al. (2005). This interpretation is further supported by the low isotope-covariance observed in the Pannonian data. As demonstrated by Li and Ku (1997), hyperalkaline lakes are expected to have poor isotope coupling due to the high DIC levels, which are little affected by freshwater discharge. Indeed, throughout the Pannonian, the $\delta^{18}\text{O}/\delta^{13}\text{C}$ covariance is poor or absent (pooled data all samples: early P.: $r^2=0.28$, middle P.: $r^2=0.04$, late P.: $r^2=0.001$), whilst coeval freshwater settings display good isotope coupling (late P.: $r^2=0.64$).

A broad array of factors may be responsible for the carbon regime. First of all, the early lake waters were strongly influenced by the heritage of the Sarmatian Paratethys Sea. This sea, as shown by Latal et al. (2004) and Piller and Harzhauser (2005), was hypersaline and carbonate-oversaturated in coastal areas. Its remaining water constituted the main component of the newly forming Lake Pannon. Beyond that primary signal, the widespread mid-Miocene ooid and coralline carbonate that formed the coasts and hinterland of the lake will have contributed to the carbonate regime of the lake. These factors may account for the high $\delta^{13}\text{C}$ values in the early Pannonian but do not fully explain the stable carbon isotope patterns during the middle Pannonian, when the lake reached its maximum extent (Magyar et al., 1999). At that time, fluvial discharge and precipitation had already contributed considerably to the water budget for more than 1 Ma and should have modified the original inherited signatures. Moreover, the middle Pannonian corresponds to the Vallesian optimum, which is characterised by high precipitation and extended wetlands (Harzhauser et al., 2004). Based on vertebrates and plant associations, the mid-Pannonian climate has been calculated by Bernor et al. (2003) and Bruch et al. (2004, in press) as warm temperate, permanently humid with warm summers and mild winters (cold month mean temperature 2–8 °C, warm month mean temperature 24–27 °C); precipitation was slightly seasonal with up to 1300 mm annual precipitation, the wettest season being the summer months. This scenario predicts a shift towards lighter $\delta^{13}\text{C}$ values. The persistently high carbon regime therefore

must have been maintained by additional factors. Such a shift towards heavy $\delta^{13}\text{C}$ values may be induced by strong stratification leading to a $\delta^{13}\text{C}$ -enriched epilimnion. High productivity and seasonal algal blooms remove ^{12}C from surface waters due to photosynthesis and will push the ^{13}C enrichment. Within that system the warm surface waters allow only little atmospheric CO_2 to be dissolved which will also support a high $\delta^{13}\text{C}$ -regime. This hypothesis is corroborated by Kováč et al. (1998), who report on middle Pannonian dinoflagellate blooms from well-cores in the Vienna Basin.

4.3. Is the Vallesian Crisis reflected in Lake Pannon's isotope record?

Our data set spans one of the most crucial and controversial turnover phases in European terrestrial environments termed the Vallesian Crisis (Agustí and Moya-Sola, 1990). Based on extinction and radiation events of mammalian faunas, this episode was originally recorded for western Europe, but is now regarded as a continent-wide event (Agustí et al., 1999; Fortelius and Hokkanen, 2001). The shifts of faunal structure were apparently triggered by climatically controlled changes of the vegetation, e.g., opening of landscapes and more deciduous trees (Agustí et al., 2003). In the surroundings of Lake Pannon, these environmental changes are reflected by the occurrence of taxa such as hyaenas, porcupines and antelopes (Harzhauser et al., 2004) and the extinction of large flying squirrels (Daxner-Höck, 2004). The turnover was discussed by Daxner-Höck (2004) to be related to increasing seasonality with drier summer months. Simultaneously, a break-up of forest environments was postulated for the late Vallesian and early Turolian based on mammal data (Bernor et al., 1996). Such a reduction of wetlands in favour of more open landscapes was also documented for the Late Miocene of the Vienna Basin by Lueger (1978) based on the composition of the terrestrial gastropod fauna and on an increase of conchyological aridity adaptations. The recorded isotope data of the middle Pannonian formed during that Vallesian optimum. Extended wetlands in a warm humid climate covered the hinterland of Lake Pannon. The late Pannonian isotope signals reflect post-crisis conditions of the Turolian. To reveal the expected shifts in isotope patterns, the three time intervals are portrayed as $\delta^{18}\text{O}/\delta^{13}\text{C}$ cross-plots (Fig. 4). This visualization allows the definition of discrete isotope fields occupied by various genera in each interval; these fields show considerable changes in shape from the early to the late Pannonian.

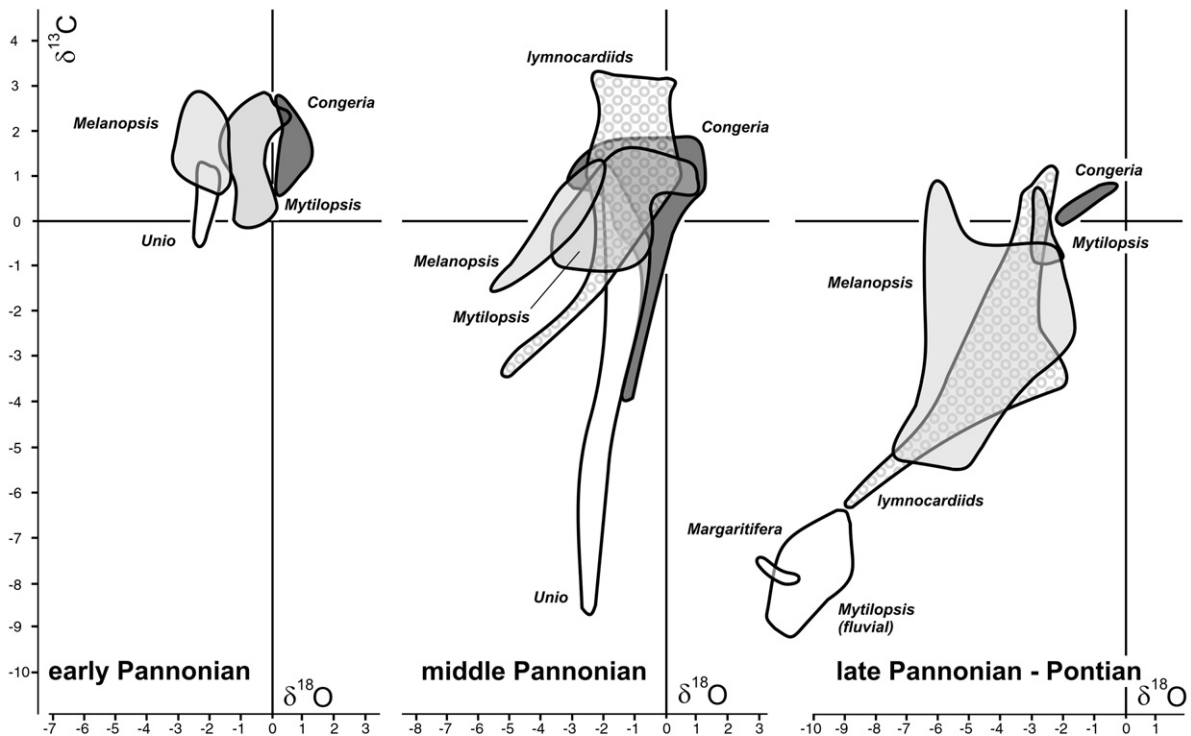


Fig. 4. Oxygen/carbon isotope cross-plots reveal the pronounced changes in isotope signals during the Pannonian. A homogeneous area is occupied by the early Pannonian values, showing only a slight grouping along the oxygen axis related to an onshore–offshore gradient. The middle Pannonian is outstanding due to its club-like fields with characteristic tails. These are interpreted to result from seasonal runoff due to enhanced precipitation. Recycling by deeper, ^{13}C -depleted water might, in addition, cause strong excursions in $\delta^{13}\text{C}$. The late Pannonian shows a comparatively simple pattern. The data gather along a mixing line from pure freshwater (light isotope values) towards lake water with higher values. The still high $\delta^{13}\text{C}$ values of lake dwellers point to persisting high-alkalinity conditions.

The early Pannonian data scatter indicates a slight onshore–offshore gradient along the oxygen axis, with fluvial–deltaic *Melanopsis* and *Unio* having lower $\delta^{18}\text{O}$ values and lake-dwelling *Congeria* having higher $\delta^{18}\text{O}$ values. The homogeneous, trendless carbon pattern displays no such ecological separation (Fig. 4). Stable conditions are also indicated by low standard deviation values in the early Pannonian (Fig. 5). Despite the strongly transgressive system of Lake Pannon at that time (Harzhauser et al., 2004), the isotope signatures are remarkably stable and homogeneous even in coastal settings. The scarcity of data with low $\delta^{18}\text{O}/\delta^{13}\text{C}$ values expected from freshwater discharge supports Lueger's (1978) observations of considerable aridity adaptations in early Pannonian terrestrial gastropods. The timing of these adaptations suggests a link with the phase-out interval of the latest Middle Miocene warming (Zachos et al., 2001), triggering low-humidity conditions around the Paratethys Sea (Piller and Harzhauser, 2005).

During the middle Pannonian, the oxygen gradient became weaker but was outbalanced by a strong increase of carbon ranges. Despite the overall high

$\delta^{13}\text{C}$ values, the middle Pannonian data are unique in showing conspicuous tails in the $\delta^{18}\text{O}/\delta^{13}\text{C}$ cross-plots (Fig. 4). Except for *Mytilopsis*, all taxa display these club-like isotope fields with heavy heads and light tails. The extension of the isotope fields in the $\delta^{18}\text{O}/\delta^{13}\text{C}$ plots is also visible in strongly increasing data variability, as indicated in the standard deviation plot (Fig. 5). A stable early Pannonian field with low σ -values is thus opposed by a well-separated, high σ -value cluster of the middle and late Pannonian. Vital effects are probably negligible in these patterns because closely related species were incorporated in all time intervals. All observed tails result from highly variable $\delta^{13}\text{C}$ values, whilst the $\delta^{18}\text{O}$ signal only affects the tails of the lymnocardiid and *Melanopsis* data-clouds. This points to two different mechanisms influencing the isotope signatures of the middle Pannonian lake waters.

Melanopsis, due to its preferred coastal–deltaic habitat, was prone to record the influx of isotopically light river water with low $\delta^{18}\text{O}$. High input of carbon-depleted material derived from decaying vegetation and/or soil weathering is reflected in the light $\delta^{13}\text{C}$ values of

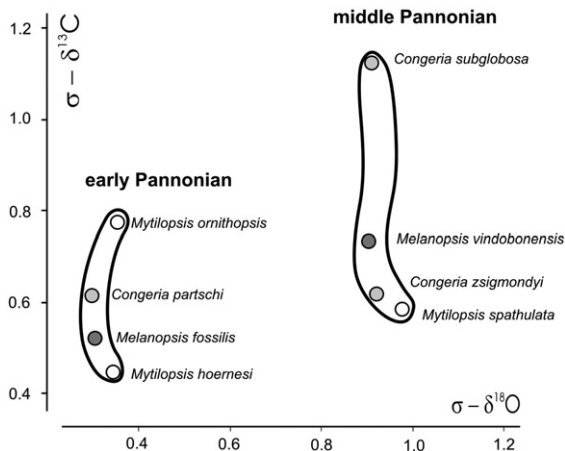


Fig. 5. Standard deviation of the data for selected taxa. Two quite homogeneous data-bunches are obvious; a low-value early Pannonian set is opposed by a well-separated group of middle Pannonian data. The discriminating factor is mainly the oxygen signature. This pattern may reflect increasing seasonal freshwater influx due to enhanced precipitation. Furthermore, a trend towards higher seasonality of temperature might have influenced this change of patterns. Such a scenario is also proposed by Bruch et al. (2004) based on palaeobotanical data.

these nearshore taxa. Similarly, the lymnocyprids follow roughly an expected mixing line from freshwater to Lake Pannon water, comparable to the simple mixing line of the late Pannon data set (Fig. 4).

In contrast, the $\delta^{13}\text{C}$ -tails of *Unio* and *Congeria* in the middle Pannonian $\delta^{18}\text{O}/\delta^{13}\text{C}$ plot cannot be related solely to freshwater discharge. They lack a strong shift in the $\delta^{18}\text{O}$ signatures which would be expected by contributions of isotopically light river runoff. These taxa were clearly mainly affected by a changing carbon regime. Extreme carbon ranges which are decoupled from oxygen values – as seen in *U. atavus* and *Congeria* – might rather be triggered by seasonal upwelling or mixing with ^{13}C -depleted deep water. This implies that the strong stratification of the lake broke down seasonally. A lack of bioturbation and abundant pyrite and marcasite in the deeper basin clays support the interpretation of a dysoxic hypolimnion. Periodic mixing events with an oxygen-rich epilimnion have also been documented by Harzhauser and Mandic (2004) based on the occurrence of very short-lived settlement phases by opportunistic dreissenids. Hence, Lake Pannon seems to have switched from an early Pannonian meromictic system into a monomictic one during the middle Pannonian.

The strange $\delta^{13}\text{C}$ -tails vanish in the late Pannonian. A pronounced onshore–offshore trend was developed. One end of the mixing line is derived from the freshwater values of *Margaritifera* and *M. neumayri*,

whilst the other is represented by *Congeria*, inhabiting deeper environments of Lake Pannon. Isotope data of *Mytilopsis* are slightly lighter than *Congeria* but well separated from the large transitional field represented by *Melanopsis* and lymnocyprids. This indicates that the latter taxa were able to settle strongly fluvial-influenced areas, which in turn reveals little about the water chemistry of Lake Pannon. This simple mixing-line model of the late Pannonian has no counterparts in the early and the middle Pannonian.

The abrupt shift of the $\delta^{18}\text{O}$ maxima (Fig. 3) towards lighter values and the overall dislocation of the isotope fields from the heavy club-head cluster of the early and middle Pannonian along a mixing-line gradient in the late Pannonian (Fig. 4) point to major changes in water chemistry. Still, the carbon regime with a peak around 0 to -1‰ (Fig. 3) supports an alkaline scenario for the pure lake settings inhabited by *Congeria*. The change seems rather to be salinity related. The middle Pannonian water of Lake Pannon is estimated to have reached salinities up to 15 psu based on the ostracod and mollusc fauna (Papp, 1953; Kovác et al., 1998), whilst a late Pannonian decline down to 5 psu was discussed by Mátyás et al. (1996) based on formation waters. This freshening is also supported by our data. Average values of single species in $\delta^{18}\text{O}/\delta^{13}\text{C}$ cross-plots show a clear trend from heavy towards lighter values during the Pannonian (Fig. 6). This trend is most pronounced along the oxygen axis and is most robust for *Melanopsis* and *Mytilopsis*.

4.4. Mollusc radiation events and isotope patterns

The initiation of the long-lived Lake Pannon was the foundation for the biggest peak in dreissenid, melanopsid and lymnocyprid evolution in the history of those molluscs. Although the endemic radiation of Pannonian molluscs is general knowledge (Papp, 1953; Magyar et al., 1999), a closer look reveals large differences in the timing of the evolutionary steps within these groups. *Melanopsis* displays its first phase of morphological disparity during the early Pannonian around 11 Ma. At that time the plasticity of the *M. impressa/fossilis* group results in an enormous number of variations (about 29 in Papp, 1953), which are difficult to handle using classical species concepts. At that time, the dreissenids experience a gradual build-up phase with about 27 taxa (Harzhauser and Mandic, in press).

In the middle Pannonian, coinciding with the onset of the carbon tails (Fig. 4), the melanopsid frenzy stops. The morphospace realized by early Pannonian melanopsids shrinks drastically and only one or two small-

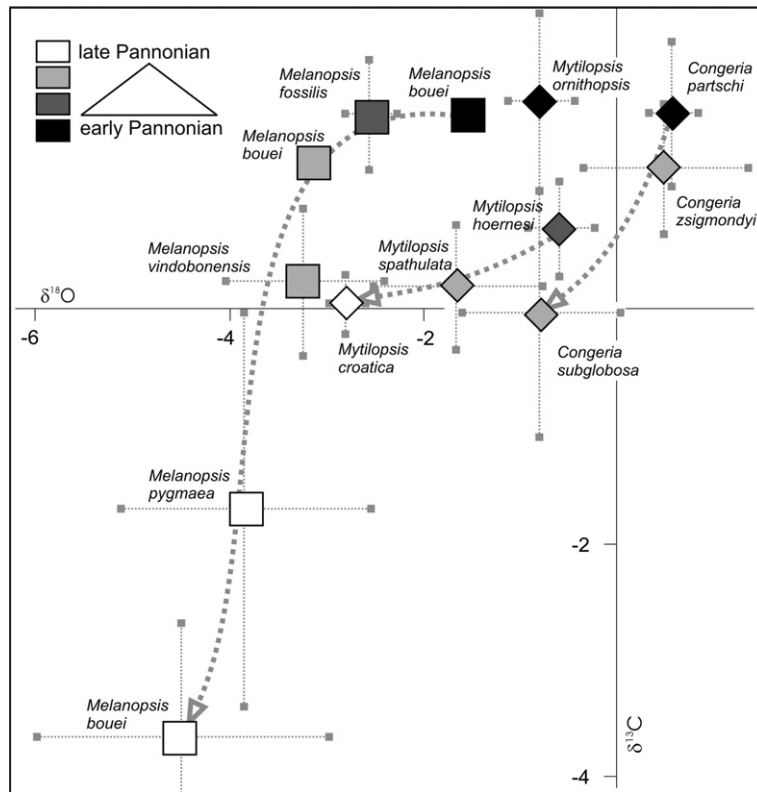


Fig. 6. Average values of single species display a clear trend from higher isotope signals in the early Pannonian to lower values in the late Pannonian. Vital effects are unlikely to influence the pattern because even specimens of the same species (e.g., *Melanopsis bouei*) follow the trend. The discriminating factor for lake dwellers such as *Mytilopsis* is mainly the oxygen isotope signal, suggesting that a freshening of the lake took place. In contrast, in deltaic *Melanopsis*, the carbon isotope signal shifts to freshwater signatures. Therefore, the carbon regime of the lake remained that of an alkaline lake, whilst freshwater runoff increasingly affected the coastal–deltaic areas during the late Pannonian.

sized species remain from the entire *M. impressa/fossilis* flock. Surprisingly, the dreissenids cross this boundary without incision, displaying instead a major evolutionary boom. Two peaks with about 44 taxa during the middle Pannonian and even 69 taxa in the late Pannonian/Pontian are documented. At the same time the range of ecological strategies of dreissenid bivalves reached a peak comprising epifaunal (*Mytilopsis*, *Dreissena*) and infaunal (dreissenomyids) filter-feeding forms and perhaps even chemosymbionts (*Congeria*).

This asynchronous evolutionary pattern hints to a mechanism which suppressed fluvial to coastal melanopsids but enhanced the radiation of sublittoral filter-feeding dreissenids. Our interpretation is a mid-Pannonian phase of advanced seasonal precipitation. Such increased precipitation within an already humid system caused periodic increases of river discharge and consequently unstable conditions in the deltaic–coastal areas inhabited by melanopsids. In the isotope record this phase is mirrored in drastically increasing variability of $\delta^{18}\text{O}$ data (Fig. 5) and by pronounced tails in the $\delta^{18}\text{O}/\delta^{13}\text{C}$ cross-

plots (Fig. 4). Whilst *Melanopsis* could not adapt to the changing environments, resulting in a diversity collapse, the filter-feeding dreissenids experienced elevated food levels. This high-precipitation scenario is corroborated by the fact that this phase also coincides with the maximum extent of Lake Pannon (Harzhauser et al., 2004).

5. Conclusions

Stable isotope analysis of Lake Pannon mollusc aragonite reveals a quickly changing hydrologic regime throughout the Late Miocene. The lake originated at about 11.6 Ma as a heritage of the alkaline, carbonate-oversaturated Paratethys Sea. It soon developed into an alkaline, probably strongly stratified lake with a highly endemic mollusc fauna. The alkaline legacy is expressed by strongly elevated $\delta^{13}\text{C}$ values. Salinity remnants, as predicted from the fauna to range around 15 psu, are indicated by the similarly high $\delta^{18}\text{O}$ values. At that time, even coastal areas are hardly affected by light isotopes from fluvial discharge, resulting in very stable

isotope fields in the $\delta^{18}\text{O}/\delta^{13}\text{C}$ cross-plots and correspondingly low variation in the data. The absence of any notable freshwater signal supports the interpretation of a reduced humidity during the early Pannonian, as also suggested by Lueger (1978) based on aridity adaptations of land gastropods. Further evidence is provided by the global curve of Zachos et al. (2001), which displays a short warming phase at the end of the Middle Miocene. This warming and dry spell is reflected in the Paratethys by a highly productive Sarmatian carbonate factory in a subtropical climate (Piller and Harzhauser, 2005). The early Pannonian was thus the phase-out interval of that low-humidity system, which allowed a tremendous radiation and increase in disparity of *Melanopsis*.

The lack of low $\delta^{13}\text{C}$ values in the frequency diagram suggests that no recycling of depleted waters from the hypolimnion took place. Throughout the Pannonian, the occurrence of unbioturbated dark blue–grey clays with high amounts of pyrite and marcasite documents the existence of such dysoxic bottom conditions.

With the onset of the middle Pannonian, conditions changed and a very humid warm climate allowed the establishment of vast wetlands in the hinterland of the lake, which now reached its maximum extension. The generally warm and humid Cfa-type climate with annual precipitation of about 1200 mm (Bernor et al., 2003; Bruch et al., 2004) coincides with the Vallesian optimum of mammal diversity with its oversaturated communities (Fortelius et al., 1996).

The isotope patterns indicate that elevated summer precipitation in the Lake Pannon catchment area caused an increase of freshwater discharge, reflected by light $\delta^{18}\text{O}$ values in nearshore taxa. Input of light carbon by rivers due to decaying plant material or soil weathering shifted the carbon regime towards light values as well. In addition, the extremely low $\delta^{13}\text{C}$ values in *Congeria* and *Unio* might have been caused by the uptake of light carbon due to periodic recirculation of depleted water from the hypolimnion. Such mixing events have already been postulated based on short-lived dreissenid settlement episodes in deeper lake settings (Harzhauser and Mandic, 2004). The seasonally changing precipitation loads are also reflected in a sudden increase of data variability (Fig. 5). These conditions substantially suppressed the radiation of *Melanopsis*, probably because this gastropod lived in deltaic–coastal areas that were maximally exposed to such runoff events. The coinciding increase in nutrient supply, however, might have been an important factor for the onset of dreissenid radiation.

The late Pannonian is characterised by a quite simple isotope pattern reflecting a predictable succession from riverine freshwater, estuarine mixing zone to open lake;

this is also reflected by the sequence from *Margaritifera* via *Melanopsis* towards *Mytilopsis* and *Congeria*. The high carbon regime remains typical for an alkaline lake, but the movement of the isotope field along the mixing line towards freshwater indicates a reduced salinity.

Our data suggest that the prevailing Cfa-type climate of the central European Late Miocene was accentuated by a low-humidity phase in the early Pannonian persisting from the latest Middle Miocene. During the middle Pannonian a considerable summer precipitation peak within an overall humid climate prevailed. The coincidence of that phase with the Vallesian optimum in mammal communities, and the abrupt change of isotope patterns in the subsequent late Pannonian (coinciding with the Vallesian crises and the early Turolian), indicates a strong climate control on the terrestrial ecosystem. A comparable link between climatically driven changes of isotope patterns and radiation pulses of the lake molluscs proves an at least equally strong climate control on the aquatic system.

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